



## Direction Reversal of Fluctuation-induced Biased Brownian Motion on Distorted Ratchets

BO YAN<sup>\*</sup>, ROBERT M. MIURA<sup>†</sup> AND YI-DER CHEN<sup>\*‡</sup>

<sup>\*</sup>*Mathematical Research Branch, National Institute of Diabetes, Digestive and Kidney Diseases, National Institutes of Health, 9000 Rockville Pike, Bethesda, MD 20892-2690, U.S.A. and*

<sup>†</sup>*Department of Mathematics, University of British Columbia, Vancouver, B.C. Canada V6T 1Z2*

(Received on 23 September 1999, Accepted in revised form on 23 October 2000)

The biased movement of Brownian particles on a fluctuating two-state periodic potential made of identical distorted ratchets is studied. The purpose is to investigate how the direction of the particle movement is related to the asymmetry of the potential. In general, distorting one of the two linear arms of a regular *symmetric* ratchet (with equal arm lengths) can create a driving force for the Brownian particle to execute biased movement. The direction of the induced biased movement depends on the type of the distortion. It has been found that if one linear arm is kinked into two linear sub-arms, the direction of the movement can be either positive or negative depending on the frequency of the fluctuation and the location and the degree of the kink. In contrast, if one arm of the symmetric ratchet is replaced by a continuous nonlinear sinusoidal function, the movement is always unidirectional. Thus, for the latter case to generate the direction reversal phenomenon, the ratchets have to have an additional asymmetry. We also have found that two potentials with different distorted ratchets can generate identical fluxes if the distortions are polar symmetric about the mid-point of the arm(s) of the basic linear two-arm ratchet. The results are useful for designing experimental apparatuses for the separation of protein particles based on their sizes and charges and the viscosity of the medium.

© 2001 Academic Press

### Introduction

A Brownian particle can be made to execute unidirectional movement in a one-dimensional periodic potential if the potential is asymmetric and the interaction between the particle and the potential field is made to fluctuate randomly or regularly among a number of potential states (Astumian & Bier, 1994; Prost *et al.*, 1994; Chauwin *et al.*, 1995; Bier & Astumian, 1996; Zhou & Chen, 1996; Chen, 1997). The fluctuation of the interaction can be produced either by

switching the potential between a number of different potential states or by changing the interaction parameter (such as the charges on the particle, if the potential field is electric) on the Brownian particle through a non-equilibrium chemical reaction (Zhou & Chen, 1996). This process could be used to separate charged particles with a fluctuating electric potential field (Rousselet *et al.*, 1994). Also this process has been suggested as a possible mechanism for generating directed movement of biological motors on linear periodic biopolymers (Astumian & Bier, 1996; Astumian, 1997; Julicher *et al.*, 1997).

To generate biased Brownian motion with a fluctuating potential, the potential must possess

<sup>‡</sup> Author to whom correspondence should be addressed.

some sort of asymmetry. For the two-state system in which the potential is switched randomly (or regularly) between a flat and a non-flat periodic potential state, the potential must be asymmetric *locally*\* in each period (Astumian & Bier, 1994; Prost *et al.*, 1994; Chauwin *et al.*, 1995; Bier & Astumian, 1996). On the other hand, if the potential fluctuates between two or more non-flat states, then the symmetry can be obtained *globally* by shifting the phases of the non-flat potentials (Chen, 1997). In this case, local asymmetry in each period is not required (Chen, 1997). The simplest periodic potential is the *regular ratchet* for which the potential in each period is shaped like a continuous sawtooth with two straight arms [see Fig. 1(a)]. This is called a *symmetric* or *asymmetric ratchet* depending on whether the arms are of equal or unequal length, respectively. An “arm-projection” asymmetry occurs when the projections of the two arms onto the horizontal axis are not equal in length. In the two-state system with a flat potential state and a regular ratchet state, the direction of the movement of the particle is completely determined by the arm-projection asymmetry, namely, to the right if the negative sloped arm of the ratchet is the longer arm and to the left if it is the shorter one. For example, a positively charged particle in Fig. 1(a) *always* moves from left to right, independent of the frequency of the fluctuation [specified by the values of  $k_1$  and  $k_2$  in Fig. 1(a)] (Astumian & Bier, 1996; Astumian, 1997; Julicher *et al.*, 1997).

Recently, it has been shown that the direction of movement in this two-state system can become frequency-dependent if one of the arms of the regular ratchet is kinked by allowing a jump in the potential at one end (Chauwin *et al.*, 1995; Chen *et al.*, 1999). That is, the direction of the particle movement in this kinked-potential case can be reversed by varying the frequency of the fluctuation (referred to as *direction reversal* or DR). It also was found that DR can occur in this system even when there is arm-projection symmetry (Chen *et al.*, 1999). This surprising result prompted us to wonder whether there exists any general rule for the generation of DR in this

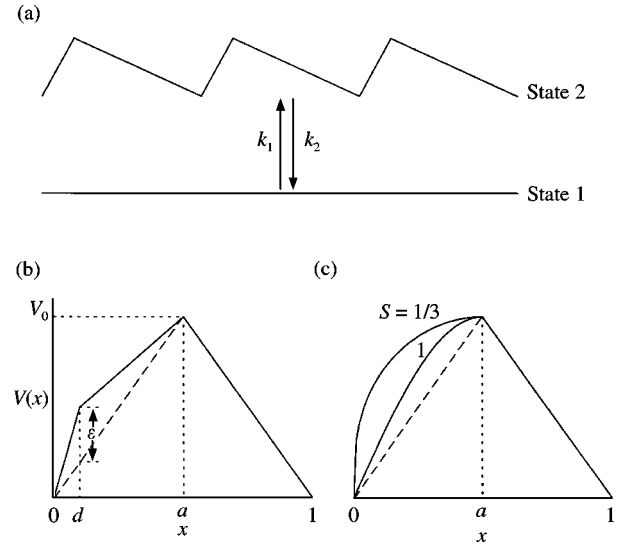


FIG. 1. (a) The two-state model with regular ratchets. (b) The regular ratchet is distorted by kinking one arm. (c) The regular ratchet is distorted by replacing one arm with a sinusoidal function,  $V(x) = V_0[\sin(\pi x/2a)]^S$ .

two-state distorted ratchet system. That is, what is the necessary condition for this two-state system to show DR? Is replacement of one of the linear arms of the ratchet with a nonlinear one sufficient to generate DR? In this case, is the arm-projection asymmetry required?

In this study, these questions were examined by carrying out numerical calculations on two special classes of distorted ratchets. Firstly, we extended our previous study (Chen *et al.*, 1999) to the case where the location of the kinked point is not restricted to the end of the arm. That is, the distortion is now characterized by two asymmetry parameters ( $\epsilon$  and  $d$ ) as shown in Fig. 1(b). Secondly, we examined the case where the left arm is replaced by a continuous sine function as shown in Fig. 1(c). We found that DR can be obtained in both cases. In the first case, DR can be obtained without the arm-projection asymmetry. In the second case, DR cannot be obtained if the arm-projection asymmetry is absent. These results suggest that the system needs at least two independent asymmetries in order to generate DR. This is the reason why the arm-projection asymmetry is required in the sinusoidal-function case.

In this study, we also found that two distinct asymmetric ratchets are able to generate identical particle fluxes if the ratchet shapes obey a special

\*Local asymmetry is determined by showing that the reflection of the potential about the location of the maximum is not symmetric.

“inversion” symmetry condition. The results obtained in this paper should be useful in designing electrophoresis setups for the separation of particles based on their sizes and charges and on the viscosity of the medium.

### Model and Mathematical Analysis

We consider the movement of a Brownian particle subjected to a one-dimensional periodic potential,  $V(x)$ , which can be switched between two potential states as shown in Fig. 1(a). In state 1, the potential is constant, and in state 2, it takes a regular ratchet shape. The rate of fluctuation between the two potential states is governed by the rate constants  $k_1$  and  $k_2$  where  $k_1$  is the rate from state 1 to state 2 and  $k_2$  is the rate from state 2 to state 1. As noted above, biased movement of the particle occurs only when some sort of asymmetry exists in the ratchet potential state. In this study, we consider the case where the left-hand side of the ratchet is replaced by a kinked piecewise linear potential defined by the position parameter,  $d$ , and the degree parameter,  $\varepsilon$ , as shown in Fig. 1(b) (Case I) or by a nonlinear function defined as  $V(x) = [\sin(\pi x/2a)]^S$  where the degree of nonlinearity parameter,  $S$ , is a constant between 0 and 1, as shown in Fig. 1(c) (Case II).

When the potential is fluctuating between two states  $i$  ( $= 1, 2$ ), the probability of finding an over-damped Brownian particle in the differential length  $dx$  centered at position  $x$  at time  $t$  is  $p_i(x, t) dx$ . The probability densities  $p_i(x, t)$  ( $i = 1, 2$ ) obey the diffusion-reaction equations

$$\frac{\partial p_1(x, t)}{\partial t} = -\frac{\partial u_1}{\partial x} - k_1 p_1 + k_2 p_2, \quad (1)$$

$$\frac{\partial p_2(x, t)}{\partial t} = -\frac{\partial u_2}{\partial x} + k_1 p_1 - k_2 p_2, \quad (2)$$

$$u_1 = -\frac{\partial p_1}{\partial x}, \quad u_2 = -\frac{\partial p_2}{\partial x} - p_2 \left( \frac{dV(x)}{dx} \right), \quad (3)$$

where  $u_i$  ( $i = 1, 2$ ) is the transport flux of the particle in potential state  $i$ , and the quantities  $x, t, V, k_1$ , and  $k_2$  have been made dimensionless. At steady state,  $\partial p_i / \partial t = 0$  and from eqns (1)–(3),

we have  $\partial u / \partial x = 0$  where  $u$  ( $\equiv u_1 + u_2$ ) is the total transport flux of the system. Note that the steady state  $u$  is a constant, independent of  $x$ . This  $u$  is equal to the *long time velocity* of the Brownian particle in the system if the steady-state probabilities satisfy the normalization condition (Zhou & Chen, 1996; Risken, 1989)

$$\int_0^1 [p_1(x) + p_2(x)] dx = 1. \quad (4)$$

Substituting eqn (3) into eqns (1) and (2) and setting the quantities on the left-hand side to zero, we obtain the differential equations for the probabilities at steady state

$$\frac{d^2 p_1(x)}{dx^2} - k_1 p_1(x) + k_2 p_2(x) = 0, \quad (5)$$

$$\begin{aligned} \frac{d^2 p_2(x)}{dx^2} + V'(x) \frac{dp_2(x)}{dx} + p_2(x) V''(x) \\ + k_1 p_1(x) - k_2 p_2(x) = 0, \end{aligned} \quad (6)$$

where  $V'(x)$  and  $V''(x)$  are the first- and second-order derivatives, respectively, of the potential in state 2.

For Case I [cf. Fig. 1(b)], the differential equations (5) and (6) in each linear region (i.e.,  $0 < x < d, d < x < a, a < x < 1$ ) have constant coefficients. As a result,  $p_1(x)$  and  $p_2(x)$  in these linear regions each can be expressed analytically as a linear combination of four linearly independent solutions, namely,

$$p_1(x) = \sum_{i=1}^4 \rho_{1i} e^{r_i x}, \quad p_2(x) = \sum_{i=1}^4 \rho_{2i} e^{r_i x}, \quad (7)$$

where  $\rho_{1i}$  and  $\rho_{2i}$  are constants and the  $r_i$  are the roots of the characteristic equation for (5) and (6):

$$\begin{vmatrix} r^2 - k_1 & k_2 \\ k_1 & r^2 + rV' - k_2 \end{vmatrix} = 0, \quad (8)$$

where  $|\cdot|$  represents a determinant. Since one root of eqn (8) is always zero, each of the sums in eqn (7) contain one constant term.

From eqn (5), it is easy to show that  $\rho_{2i}$  can be expressed in terms of  $\rho_{1i}$  as

$$\rho_{2i} = [k_1 - r_i^2] \rho_{1i} / k_2. \quad (9)$$

Thus, only four constants in eqn (7) are unknown in each linear region. As a result, there are a total of 12 unknown constants to be determined [because there are three smooth regions of  $V$  in the system, see Fig. 1(b)]. At steady state, both  $p_1(x)$  and  $p_2(x)$  as well as  $u_1$  and  $u_2$  are continuous at  $x = 0, d$ , and  $a$ . Thus, there are 12 boundary conditions that could be used for the determination of the 12 unknowns in eqn (7). However, these 12 boundary conditions are not independent; one of them has to be replaced by the normalization condition in eqn (4). The evaluation of the constants  $\rho_{1i}$ , etc. in eqn (7) involves the solution of a system of 12 linear algebraic equations and can be carried out easily using Mathematica. After obtaining  $p_1(x)$  and  $p_2(x)$ , the velocity of the Brownian particle can be calculated from eqn (3).

For Case II in Fig. 1(c) where the potential in state 2 is partly nonlinear, the above mathematical procedure is not applicable. In this case, the solution of eqns (5) and (6) was obtained approximately using a finite-difference method (Zhou & Chen, 1996; Chen, 1997).

## Results

For the results presented here,  $V_0$  is set to 10, and the rate constants of switching between the two potential states are assumed to be equal ( $k_1 = k_2 = k$ ), unless otherwise specified. We first discuss the kinked case (I) and then the continuous case (II).

For the kinked case, the asymmetry of the system is determined by the values of  $\varepsilon$  (the degree of the kink),  $d$  (the position of the kink on the  $x$ -axis), and  $a$  (the position of the peak of the original sawtooth that defines the arm-projection asymmetry). We consider three values of  $a = 0.48, 0.5, 0.52$  and five values of  $d = 0.01, 0.1, a/2, a - 0.1$ , and  $a - 0.01$  and set the value of  $k$  to 1. Fig. 2(a) shows the plots of  $u$  as a function of  $\varepsilon$  for  $a = 0.5$  (the case with the arm-projection symmetry). Firstly, it is obvious from the plot that each flux curve passes through the origin at  $\varepsilon = 0$

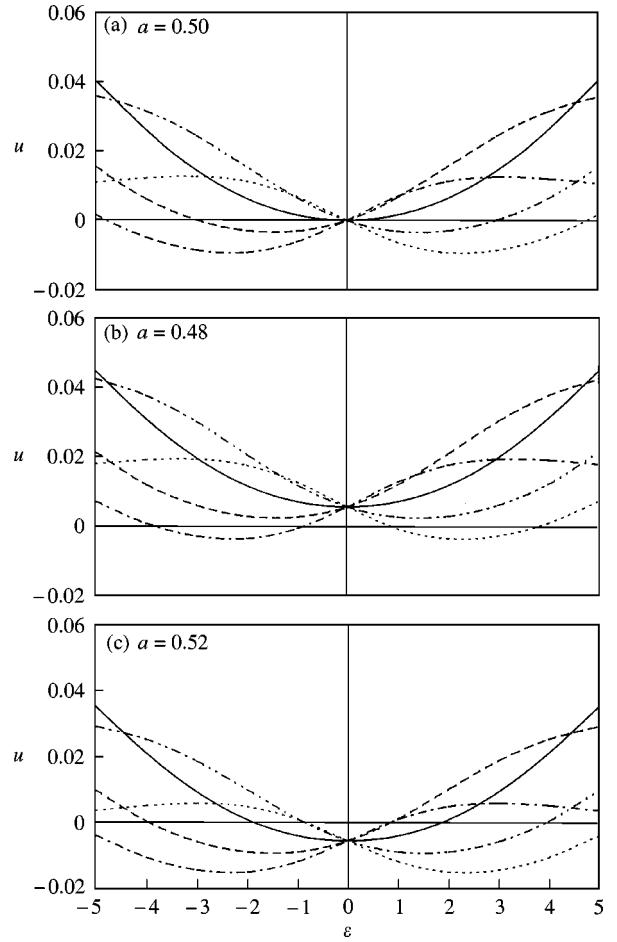


FIG. 2. Calculated transport fluxes as a function of  $\varepsilon$  at  $k_1 = k_2 = k = 1$  for  $a = 0.5$  (a),  $0.48$  (b), and  $0.52$  (c) and several values of  $d$ . The meanings of  $\varepsilon$ ,  $a$ , and  $d$  are defined in Fig. 1(b): (.....)  $d = 0.01$ ; (-.-.-)  $0.10$ ; (—)  $a/2$ ; (- - -)  $a - 0.10$ ; (- - -)  $a - 0.01$ .

and  $u = 0$ . This is due to the fact that the local asymmetry of the potential disappears when  $\varepsilon = 0$  at  $a = 0.5$  [see Fig. 1(b)]. Secondly, if  $d = a/2 = 0.25$ , the flux  $u$  is always positive for  $\varepsilon \neq 0$ , independent of the sign  $\varepsilon$  (see the solid curve), that is, the particle always moves to the right no matter whether the kink is up or down. On the other hand, if  $d \neq 0.25$ , then there is always a region in  $\varepsilon$  where the flux is negative (i.e., the particle moves to the left). One end of this negative  $u$  region is located at  $\varepsilon = 0$ , and the other end is located at some positive  $\varepsilon$  if  $d < 0.25$  and at some negative  $\varepsilon$  if  $d > 0.25$ . Thus, unless  $d$  is exactly equal to  $0.25$ , the direction of net movement of the Brownian particle will change from right to left and back to right again as the value of  $\varepsilon$  is varied from very negative to very

positive values (or vice versa). Thirdly, as can be seen in Fig. 2(a), the flux curve for  $d = 0.01$  is exactly the mirror image of the flux curve for  $d = a - 0.01$  with respect to the line  $\varepsilon = 0$ . Thus, in general, we have

$$u(\varepsilon, d) = u(-\varepsilon, a - d). \quad (10)$$

That is, the potential with an upward kink of  $\varepsilon$  at  $d$  will generate a transport flux identical to that generated by the potential with a downward kink of the same amount at  $a - d$ . In the  $(x, V)$ -plane of Fig. 1b, the coordinates of the two kinked points at  $d$  and  $a - d$  can be shown to be  $(d, \varepsilon + V_0 d/a)$  and  $(a - d, V_0 - [\varepsilon + V_0 d/a])$ , respectively. It is easy to see that these two points have polar symmetry about the point  $(x, V) = (a/2, V_0/2)$ . In other words, two periodic potentials with kinked ratchets such as shown in Fig. 1b will generate identical fluxes if the kink points are symmetrical about the point  $(a/2, V_0/2)$  (the inversion symmetry principle).

The flux curves calculated for  $a = 0.48$  and  $0.52$  are plotted in Figs. 2(b) and 2(c), respectively. As shown in the figures, the common intercepts at  $\varepsilon = 0$  are not at  $u = 0$  in these two cases because the original regular ratchets have the arm-projection asymmetry. In general, the curves in Figs. 2(b) and 2(c) are almost identical to those in Fig. 2(a) if the three common intercepts at  $\varepsilon = 0$  are forced to coincide. This implies that contributions to the biased Brownian motion

from the arm-projection and the kink asymmetries are approximately additive in this two-state model. As can be seen in Figs. 2(b) and 2(c), the system also obeys the inversion symmetry principle. That is, the inversion symmetry property of the flux is not affected by the value of  $a$ .

To examine the effect of the fluctuation rate between the two potential states on the movement of the particles, the transport fluxes  $u(\varepsilon)$  are calculated at three values of  $k$  for the case  $a = 0.5$  and  $d = 0.1$  and are plotted in Fig. 3. As shown in the figure, increasing the rate constant  $k$  decreases the interval in  $\varepsilon$  over which  $u$  is negative. This implies that if the transport flux is negative at small  $k$ , then it can change sign when the frequency is increased (the direction reversal (Chauwin *et al.*, 1995; Chen *et al.*, 1999)). This is demonstrated clearly in Fig. 4 where  $u$  is plotted

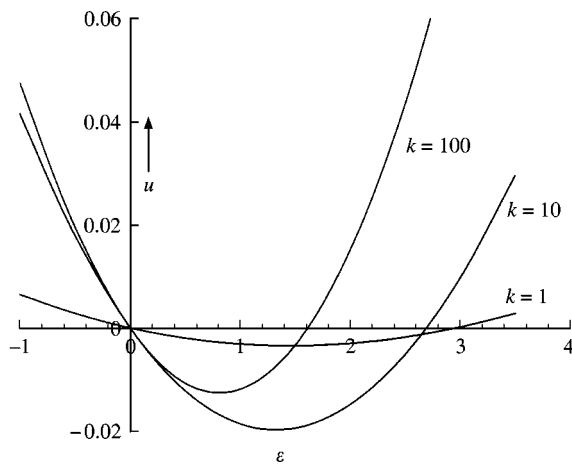


FIG. 3.  $u(\varepsilon)$  at different values of  $k$  for  $a = 0.5$  and  $d = 0.1$ . As  $k$  increases, the critical  $\varepsilon$  at which  $u$  changes sign from negative to positive becomes smaller.

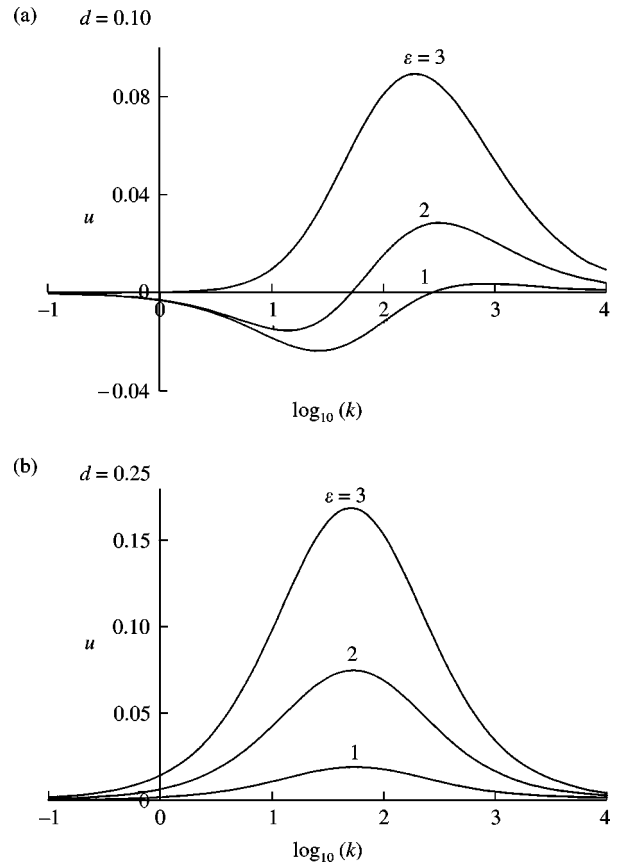


FIG. 4. Transport flux as a function of the fluctuation frequency showing the direction-reversal phenomenon for the case  $a = 0.5$ . (a)  $d = 0.1$ . Direction reversal occurs only when  $\varepsilon < 3$  (i.e., the kink is less than  $0.3 V_0$ ). (b)  $d = 0.25$  ( $\equiv a/2$ ). Direction reversal is absent for any degree of the kink.

as a function of  $\log k$  for  $a = 0.5$ , two values of  $d$ , and three values of  $\varepsilon$ . For example, for the  $d = 0.1$  case, the flux at  $\varepsilon = 1$  is negative at small  $k$ . As  $k$  increases, the flux first decreases, reaches a minimum, then increases and changes its sign, reaches a maximum, and then decreases, as shown in Fig. 4(a). On the other hand, if the flux is positive at small  $k$ , increasing the value of  $k$  will only change the magnitude of the flux, not the sign, as shown in the  $\varepsilon = 3$  curve in Fig. 4(a) and in all curves in Fig. 4(b) for the  $d = 0.25$  case.

The results in Figs. 2 and 3 imply that the coordinates of the kinked point (characterized by the values of  $d$  and  $\varepsilon$ ) in the  $(x, V)$ -plane can be grouped into positive- and negative-velocity regions (or domains) as shown in Fig. 5. In general, the negative-velocity domains are symmetric with respect to the mid-point of the arm of the original ratchet at  $(x, V) = (a/2, V_0/2)$ . The shapes and the sizes of the domains depend on the frequency of the fluctuation. As shown in Fig. 5, as  $k$  increases, the area of negative  $u$  decreases. The shape of the phase diagram also is greatly influenced by the value of  $a$ . When  $a$  is equal to 0.5, one of the boundaries of the negative  $u$  domain is always along the arm of the (unkinked) symmetric ratchet, and the negative phase is divided into two sub-domains that are joined at the center of symmetry at  $(x, V) = (a/2, V_0/2)$  [see Fig. 5(a)]. For  $a$  less than 0.5, the two negative  $u$  sub-domains become disjoint [see Fig. 5(b)]. Finally, for  $a$  greater than 0.5, the negative  $u$  domain occurs as a single connected region [see Fig. 5(c)]. It is important to point out that, as shown in the figures, the value of  $k$  affects only the area and the shape of each domain or sub-domain, but not the number or the connectivity of the domain(s). The phase diagrams in Fig. 5 are very useful in determining whether or not a particular potential will generate the direction-reversal phenomenon. For example, the point indicated by an asterisk in Fig. 5(a) is located inside the negative phase for  $k = 1$  and 10 (the border for this case is not shown in the figure), but is located outside that for  $k = 100$ . Thus, a particle in this potential will move towards the left (negative  $u$ ) at small  $k$  and change its direction ( $u$  becomes positive) when  $k$  becomes greater than 100.

We also carried out the calculations for the case that  $k_1$  is fixed at 0.01 (the same case as we

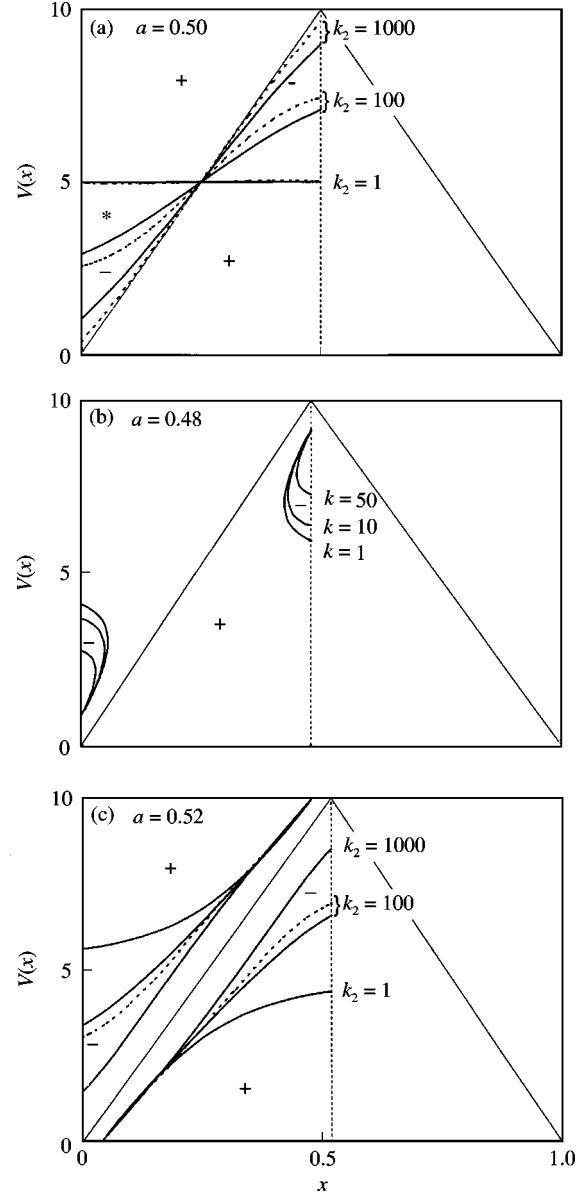


FIG. 5. The phase diagram showing the sign (or direction) of the velocity of the Brownian particle as a function of the coordinates of the kinked point of a distorted ratchet in the  $x$ - $V$  coordinate system at different  $k_1$  and  $k_2$  values. The triangle in thin lines is the original undistorted ratchet. Negative (—) velocity means that the Brownian particle is moving toward the negative  $x$  (left) direction and vice versa. In general, the kinked points can be divided into two bounded regions with positive and negative velocities, respectively. Increasing the rate constants (or frequency of the fluctuation) decreases the area of the negative region. (a) The  $a = 0.5$  case. The negative velocity region is bounded by the arm of the original ratchet and the solid or the dashed curve shown in the figure and is divided into two symmetric domains connected at  $(x, V) = (a/2, V_0/2)$ , the mid-point of the original undistorted ratchet arm. (b) The  $a = 0.48$  case. The negative velocity region for any given  $k$  is divided into two disconnected domains which are symmetrical about the point at  $(x, V) = (a/2, V_0/2)$ . (c)  $a = 0.52$ . The negative velocity region is connected. The inversion symmetry holds for the entire region. (.....)  $k_1 = 0.01$ ; (—)  $k_1 = k_2$ .

did before (Chen *et al.*, 1999). Direction reversal (DR) was also found in this case. The phase diagrams showing the coordinates of the kinked points with negative velocities evaluated at some values of  $k_2$  are also shown in Fig. 5(a) and 5(c) for  $a = 0.5$  and  $0.52$ . When the dashed curves ( $k_1 = 0.01$ ) are compared with the solid curves ( $k_1 = k_2$ ) in Fig. 5(a) and 5(c), it is easy to see that, for the same  $k_2$ , reducing the value of  $k_1$  decreases the area of the negative velocity region in the phase diagram. However, the shapes of the phase diagrams evaluated at different  $a$  values for this  $k_1 = 0.01$  case are very similar to those for the  $k_1 = k_2$  case. This implies that the *existence* of DR in this two-state model is determined only by the shape and the asymmetry of the kinked potential, not by the frequency of the fluctuation. Although the mechanism underlying the generation of DR is hard to get for the  $k_1 = k_2$  case, a qualitative explanation can be obtained for the  $k_1 = 0.01$  case based on the same physical arguments discussed before by Chen *et al.* (1999).

For Case II, the potential on the left half of the ratchet is replaced by the nonlinear function  $V(x) = V_0[\sin(\pi x/2a)]^S$  where  $0 \leq x \leq a$  and  $0 < S \leq 1$ . The potential becomes more distorted as the value of  $S$  becomes smaller [see Fig. 1(c)]. In Fig. 6(a), the calculated transport fluxes for  $a = 0.5$  are plotted as a function of  $S$  for  $k = 1, 10$ , and  $100$ . As shown in the figure, the induced flux is always positive and is independent of the values of  $k$  and  $S$ . That is, no DR is expected in this case. It is easy to show that  $V(x) = V_0(1 - [\cos(\pi x/2a)]^S)$  and  $V(x) = V_0[\sin(\pi x/2a)]^S$  are polar symmetric with respect to each other about the inversion point  $(x, V) = (a/2, V_0/2) = (0.25, V_0/2)$ . Thus, one would expect the two functions to give the same transport flux if the “inversion symmetry” principle found for the kinked case discussed above is applicable to this case also. This indeed is correct; the calculated transport curves for the cosine case are identical to those in Fig. 6(a) for the same values of  $k$  and  $S$ . In other words, the inversion symmetry principle seems to apply irrespective of whether the potential is continuous or kinked.

The result that particle movement is always biased to the right when the left arm of the original symmetric ratchet is replaced by the nonlinear sine function implies that this specific

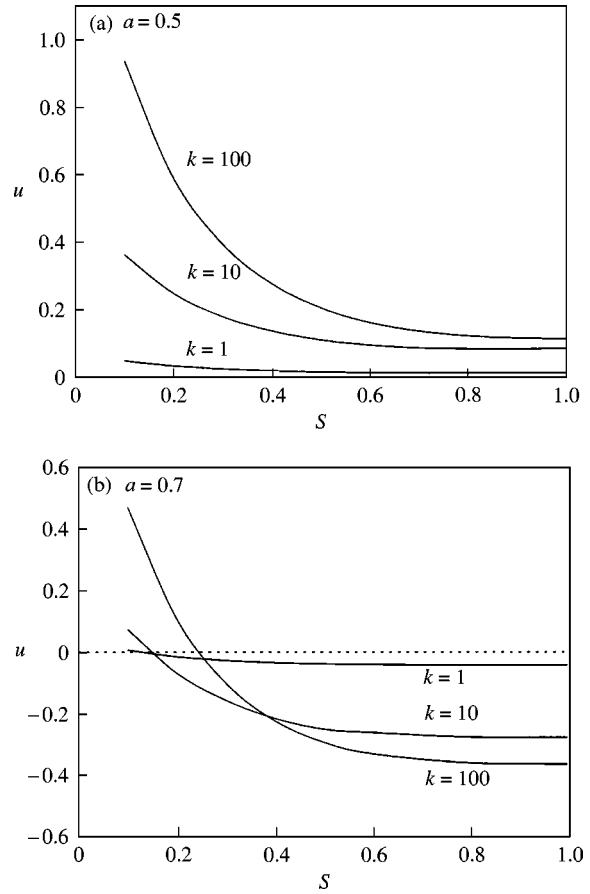


FIG. 6. The flux curves calculated for the two-state model with the distorted potential shown in Fig. 1(c), in which the left arm of the regular ratchet is replaced by the nonlinear sinusoidal function,  $V(x) = V_0[\sin(\pi x/2a)]^S$ . (a)  $a = 0.5$ . (b)  $a = 0.7$ .

nonlinearity in the left arm of the ratchet creates a driving force for the particle to move toward the right. As mentioned before, the arm-projection asymmetry can generate a driving force for the particle to move toward the left if the right arm-projection is shorter than the left one, i.e., when  $a > 0.5$ . Thus, by adjusting the value of  $S$  and  $a$ , the sign of the flux can be varied. This is indeed the case as one can see from Fig. 6(b) in which the flux at different values of  $k$  is plotted as a function of  $S$  for  $a = 0.7$ . This result implies that DR is possible when the projection on the  $x$ -axis of the nonlinear sine function arm in Fig. 1(c) is longer than that of the linear arm. The phase diagram showing the regions of positive and negative velocities of the particle on the  $(S, a)$  plane as a function of  $k$  are shown in Fig. 7. With this diagram, it is easy to determine whether

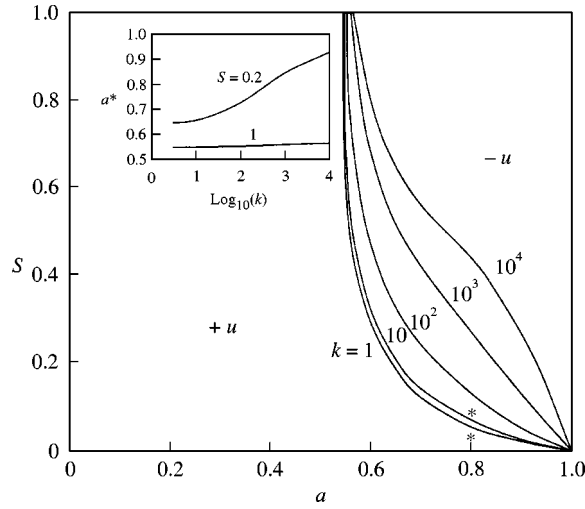


FIG. 7. The phase diagram showing the dividing line between the regions of positive and negative fluxes on the  $(S, a)$  plane as a function of  $k$ .

a particular nonlinear sine function ratchet is capable of generating DR. For example, ratchets with  $S = 0.04$  and  $a = 0.8$  will not generate DR if  $k > 1$ , while those with  $S = 0.1$  and  $a = 0.8$  will generate DR between  $k = 10$  and  $100$  [compare the positions of the two points indicated by stars (\*) in Fig. 7].

### Discussion

The main purpose of this paper has been to investigate the relationship between the local asymmetry of the ratchets in a periodic potential and the direction of movement of a Brownian particle when the potential is switching on-and-off randomly between two potential states, one of which is flat. We have found that in the absence of any other asymmetries, distorting one arm of the linear regular ratchet in the periodic potential can create a driving force for the particle to execute biased movement. The direction of the biased movement depends on the type of distortion. For example, if the distortion is made by kinking one arm as shown in Fig. 1(b) (Case I), the induced biased movement can be positive or negative depending on the position ( $d$ ) and the degree ( $\varepsilon$ ) of the kink [see Fig. 2(a)]. On the other hand, if one arm (of the symmetric regular ratchet) is replaced by the sinusoidal function shown in Fig. 1(c) (Case II), then the direction of biased

movement of the particle is always from the left to the right [see Fig. 6(a)]. Thus, in order to generate DR, the ratchets may or may not require the arm-projection asymmetry in Case I, as has been found in our calculations. In contrast, the arm-projection asymmetry is definitely required in Case II in order for the system to generate DR.

Systems exhibiting the direction reversal (DR) phenomenon have been reported before by several investigators. Kula *et al.* (1998) found that DR could be obtained if the particle was subjected to a non-equilibrium fluctuating force. Millonas and Dykman (1994) discussed a stationary periodic potential in which the generation of DR is induced by a Gaussian force noise with a non-white power spectrum. Reimann and Elston (1996) discussed the generation of DR in a general periodic potential with non-Gaussian dichotomous force noise. Bier and Astumian (1996) showed that DR could be obtained in a special fluctuating three-state ratchet model. Chauwin *et al.* (1995) were the first to find that the direction reversal could be obtained in the two-state model in Fig. 1(a) if the long arm of the ratchet is kinked vertically at the end [corresponding to  $d = 0$  and  $a > 0.5$  in Fig. 1(b)]. Recently, we showed that the existence of the frequency-dependent DR in the two-state model of Chauwin *et al.* does not depend on whether  $a$  is larger than, equal to, or smaller than  $0.5$  (Chen *et al.*, 1999). Here we have shown that DR can be achieved in this system even when the value of  $d$  in Fig. 1(b) is not equal to zero (that is, the kink is not restricted to the end of the arm).

The phase diagrams showing the exact relationship between the asymmetry parameters of the potential and the sign of the flux are given in Fig. 5 for Case I and in Fig. 7 for Case II. These diagrams can be used to determine whether a particular ratchet geometry will generate the direction reversal phenomenon and should be useful in designing the apparatus for particle separation based on the two-state system described in this paper.

One unexpected result of this study is the finding that the transport fluxes of two distorted nonlinear ratchet potentials are equal if the two distortions have polar symmetry about the midpoint of the arm of the original regular ratchet.



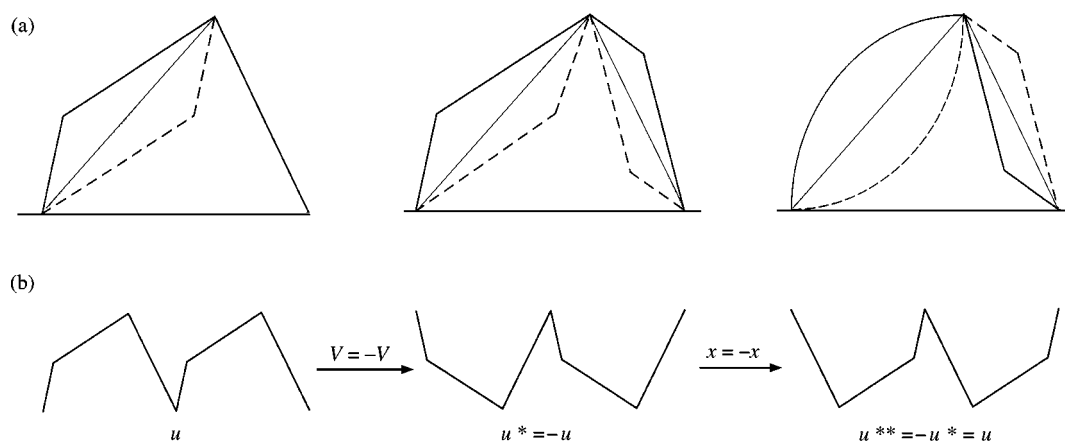


FIG. 8. (a) Equivalent distorted ratchet potentials that produce equal fluxes. The potential defined by the solid lines is said to be equivalent to that defined by the dotted lines in each figure because they are symmetrical to each other about the mid-point of both arms of the original regular ratchet (see text). (b) Relationship between the sign of the flux (or the direction of the movement) and the inversion operations applied to the entire periodic potential. The inversion operations affect only the sign of the flux, not the magnitude of the flux. Note that the last potential diagram is identical to the first one with the dotted line in (a).

That is, two different distorted ratchet potentials can be considered to be equivalent with respect to transport flux if one distortion is the “inverted image” of the other about the mid-point of the arm of the undistorted ratchet. This “inversion symmetry principle” also holds when distortions are applied to both arms. For example, the potential given by the solid lines in each figure in Fig. 8(a) is equivalent to that given by the dashed lines, and therefore, both potentials will produce identical fluxes. This principle is very general in that the distortion can be of any shape. The correctness of the principle can be explained by the following simple argument. As shown in Fig. 8(b), let us carry out two inversion operations on the periodic non-flat potential: (1) change the sign of the potential,  $V(x) \rightarrow -V(x)$ ; and (2) change the sign of the potential axis,  $x \rightarrow -x$ . It is obvious that each operation will change the sign, but not the magnitude, of the flux. As a result, the flux will remain invariant after the two operations. Now, if one examines the shape of the potential after the two operations, then one will find that the resultant potential is identical to the “inverted” potential of the original ratchet potential [compare the last diagram in Fig. 8(b) with the first one in Fig. 8(a) given by the dashed lines]. This proves that equivalent distorted ratchet potentials with inversion symmetry will produce equal fluxes in

a two-state model. The same argument can be applied to cases where both arms of the ratchet are distorted.

One author (RMM) wishes to acknowledge research funding from the Natural Sciences and Engineering Research Council of Canada. Also, he thanks Drs Alwyn Scott, Mads Soerensen, and Peter Christiansen of the Department of Mathematical Modelling, Technical University of Denmark for their hospitality and support during part of this research.

## REFERENCES

- ASTUMIAN, R. D. (1997). Thermodynamics and kinetics of Brownian motor. *Science* **276**, 917–922.
- ASTUMIAN, R. D. & BIER, M. (1994). Fluctuation driven ratchets: molecular motors. *Phys. Rev. Lett.* **72**, 1766–1769.
- ASTUMIAN, R. D. & BIER, M. (1996). Mechanochemical coupling of the motion of molecular motors to ATP hydrolysis. *Biophys. J.* **70**, 637–653.
- BIER, M. & ASTUMIAN, R. D. (1996). Biasing Brownian motion in different directions in a 3-state fluctuating potential and an application for the separation of small particles. *Phys. Rev. Lett.* **76**, 4277–4280.
- CHAUWIN, J.-F., AJDARI, A. & PROST, J. (1995). Current reversal in asymmetric pumping. *Europhys. Lett.* **32**, 373–378.
- CHEN, Y. (1997). Asymmetric cycling and biased movement of Brownian particles in fluctuating symmetric potentials. *Phys. Rev. Lett.* **79**, 3117–3120.
- CHEN, Y., YAN, B. & MIURA, R. M. (1999). Asymmetry and direction reversal in fluctuation-induced biased Brownian motion. *Phys. Rev. E* **60**, 3771–3775.

- JULICHER, F., AJDARI, A. & PROST, J. (1997). Modeling molecular motors. *Rev. Mod. Phys.* **69**, 1269–1281.
- KULA, J., CZERNIK, T. & LUCZKA, J. (1998). Brownian ratchets: transport controlled by thermal noise. *Phys. Rev. Lett.* **80**, 1377–1380.
- MILLONAS, M. M. & DYKMAN, M. I. (1994). Transport and current reversal in stochastically driven ratchets. *Phys. Lett. A* **185**, 65–69.
- PROST, J., CHAUWIN, J.-F., PELITI, L. & AJDARI, A. (1994). Asymmetric pumping of particles. *Phys. Rev. Lett.* **72**, 2652–2655.
- REIMANN, P. & ELSTON, T. C. (1996). Krammers rate for thermal plus dichotomous noise applied to ratchets. *Phys. Rev. Lett.* **77**, 5328–5331.
- RISKEN, H. (1989). *The Fokker-Planck Equations*. Berlin: Springer-Verlag.
- ROUSSELET, J., SALOME, L., AJDARI, A. & PROST, J. (1994). Directional motion of Brownian particles induced by a periodic asymmetric potential. *Nature* **370**, 446–448.
- ZHOU, H.-X. & CHEN, Y. (1996). Chemically driven motility of Brownian particles. *Phys. Rev. Lett.* **77**, 194–197.